

1 **Spatio-temporal models provide new insights on the biotic and abiotic drivers shaping Pacific**  
2 **Herring (*Clupea pallasii*) distribution**

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24 **ABSTRACT**

25 Determining how fish respond to variation in biotic and abiotic conditions is a crucial prerequisite  
26 to forecasting changes in productivity and spatial distribution of fish stocks and designing  
27 sustainable marine resource management strategies. In the present study, we investigated the  
28 physical and biological drivers of the spatio-temporal dynamics of Pacific Herring (*Clupea pallasii*),  
29 which is a marine forage fish species important for commercial fisheries and First Nations in the  
30 northeastern Pacific. We fit multivariate spatio-temporal models to fisheries-independent trawl-  
31 and acoustics-based data collected off the West Coast of Vancouver Island (WCVI), Canada,  
32 during summers over the period 2006-2014. We evaluated the effects of the main ocean  
33 environmental drivers of WCVI lower trophic level productivity, including sea surface  
34 temperature (SST), chlorophyll *a*, fluorescence, salinity, oxygen, transmissivity and zooplankton  
35 density on variation in Pacific Herring biomass. Models were also used to measure spatio-  
36 temporal covariation with other pelagic, semi-pelagic, and bottom-associated fish species  
37 occurring off the WCVI to address potential competitive and predation interactions. Through  
38 application of these spatio-temporal models we found: (i) Pacific Herring biomass off the WCVI  
39 increased during 2006-2014; the highest Pacific Herring biomass was repeatedly found on the  
40 continental shelf (depths < 185m) while low densities were usually observed along the shelf break  
41 (depths > 185m), where Euphausiids, Pacific Hake, Sablefish and Arrowtooth Flounder were more  
42 abundant, which could reflect predation avoidance behaviour; (ii), the local biomass of Pacific  
43 Herring was related quadratically to the average SST in May; (iii) a positive covariation in spatio-  
44 temporal densities between Pacific Herring and its common zooplankton prey, supporting a  
45 potential bottom-up control hypothesis; (iv) a negative covariation in spatio-temporal densities  
46 between Pacific Herring and both Pacific Hake and Pacific Sardine, which could reflect predation  
47 and competitive interactions, respectively; and (v) a positive covariation in spatio-temporal  
48 densities between Pacific Herring and several groundfish species (i.e., Arrowtooth Flounder,  
49 Sablefish, Pacific Halibut, Pacific Cod), which suggests these predators may have less impact on  
50 Pacific Herring mortality than Pacific Hake, and highlights the need for an accurate reassessment  
51 of the relative contribution of those species to the total summer predation pressure experienced

52 by Pacific Herring off the WCVI. The findings of this study contribute to a better understanding  
53 of the WCVI marine ecosystem.

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## 74 INTRODUCTION

75 Spatio-temporal dynamics of low-trophic-level fish (i.e., ‘forage fish’) can have a strong  
76 impact on commercial fisheries, the sustainability of ecosystems, and the conservation of  
77 sensitive species (Pikitch et al. 2014). There is now a growing body of evidence suggesting that  
78 many marine ecosystems are currently experiencing an ongoing overall decline in forage fish  
79 abundance caused by overfishing, other human activities and environmental change, which in  
80 turn impacts higher trophic level species, resulting in further negative socio-economic and  
81 environmental consequences (Pinsky et al. 2011, Smith et al. 2011). In a rapidly changing ocean,  
82 understanding and forecasting the response of forage fish to environmental conditions and  
83 ecosystem change is thus a desirable component of the design of sustainable management  
84 strategies for marine resources.

85 Pacific Herring (*Clupea pallasii*) is a pelagic forage fish species widely distributed in the  
86 northeast Pacific, from California to the Bering Sea (Rounsefell 1930, Miller & Schmidtke 1956,  
87 Wespestad & Fried 1983). There is a long-standing interest in Pacific Herring biology and ecology  
88 as this species generates large economic benefits for commercial fisheries and is a key species in  
89 First Nations communities and cultures in the northeast Pacific (Taylor 1964, Schweigert et al.  
90 2009, DFO 2018). Moreover, Pacific Herring are a substantial part of the diet of many other  
91 commercially-important fish and marine mammal species and, thus, also occupy a key position  
92 in marine ecosystems and trophic webs (Purcell & Grover 1990, Livingston 1993, Schweigert et  
93 al. 2010). In British Columbia (BC), Canada, Pacific Herring are assessed as five major and two  
94 minor stocks defined by spawning area (Stocker 1993, DFO 2018). They are a relatively short-  
95 lived (~10 years), migratory species; immature and adult herring typically feed on zooplankton  
96 (e.g., copepods, Euphausiids, etc.) on the continental shelf in the summer before spawning in  
97 nearshore areas in early spring (Wailes 1936, Hay 1985). Additionally, Pacific Herring from  
98 different stocks forage together in common areas in summer months. For example, both the  
99 West Coast of Vancouver Island (WCVI) and Strait of Georgia (SOG) spawning stocks of Pacific  
100 Herring forage in a common area off the southwest coast of Vancouver Island during the summer,  
101 before migrating to their respective spawning grounds in winter (Taylor 1964).

102            Since the beginning of commercial fishing for Pacific Herring in BC in the late 19<sup>th</sup> century  
103 (Taylor 1964, Pearse & others 1982), stocks have experienced two main collapses, the first in the  
104 1930s and the second in the 1960s, both followed by fishery closures and fairly rapid stock  
105 recovery of some, but not all, areas (Hourston 1978, Ware 1991). After the 1970s-1980s, the  
106 biomass of some stocks, notably the Haida Gwaii and WCVI stocks, declined back to near-collapse  
107 levels of the 1960s, with no clear signs of subsequent recovery despite commercial fishery  
108 closures (Schweigert et al. 2010, DFO 2018). Age-structured stock assessment estimates of WCVI  
109 Pacific Herring natural mortality have generally increased since the late 1970s (DFO 2018).  
110 Although many authors have addressed this topic (Tester 1948, Ware 1991, Schweigert 1995,  
111 Schweigert et al. 2010), spatio-temporal fluctuations of Pacific Herring stocks in relation to biotic  
112 and abiotic factors are not fully understood. Understanding these relationships is particularly  
113 challenging as environmental conditions, top-down regulation, and bottom-up drivers of Pacific  
114 Herring abundance presumably interplay in complex ways and can vary among regions and  
115 ecosystems.

116            Predation is often thought to drive spatio-temporal fluctuations in Pacific Herring stocks,  
117 given that this species constitutes a substantial part of the diet of several marine mammals and  
118 predatory fish, e.g., Humpback Whales (*Megaptera novaeangliae*), Pacific Hake (*Merluccius*  
119 *productus*), Lingcod (*Ophiodon elongatus*), Pacific Cod (*Gadus macrocephalus*), Sablefish  
120 (*Anoplopoma fimbria*), Arrowtooth Flounder (*Atheresthes stomias*), Pacific Halibut (*Hippoglossus*  
121 *stenolepis*), and Chinook (*Oncorhynchus tshawytscha*) and Coho (*O. kisutch*) Salmon (Brodeur  
122 1991, Ware & McFarlane 1995, Pearsall & Fargo 2007, Duffy & Beauchamp 2011). For example,  
123 Ware & McFarlane (1986, 1995) estimated that three predatory fish species (e.g. Pacific Hake,  
124 Sablefish and Pacific Cod) could annually consume *ca.* 29-54 % of the Pacific Herring foraging off  
125 the WCVI. Similarly, in a study reviewing factors limiting recovery of Pacific Herring, Schweigert  
126 et al. (2010) estimated that *ca.* 54% of the Pacific Herring foraging off the WCVI could be  
127 consumed annually by predatory fish and marine mammals. Interestingly, however, Schweigert  
128 et al. (2010) found that predation pressure on Pacific Herring shifted from fish species to marine  
129 mammals in the late 20<sup>th</sup> century. However there was no strong positive association between  
130 Pacific Herring mortality and predation intensity, suggesting that the lack of recent recovery of

131 WCVI Pacific Herring may be driven by other factors.

132           Competition for resources with Pacific Sardines (*Sardinops sagax*) has been suggested as  
133 one factor driving fluctuations in WCVI Pacific Herring stocks (Schweigert 1995, Schweigert et al.  
134 2010), since both species share common prey and occupy similar habitats (McFarlane et al. 2005).  
135 Herring mortality has been shown to be positively associated with sardine biomass in the  
136 California Current over the period 1973-2008, providing additional support to the competition  
137 hypothesis (Schweigert 1995, Schweigert et al. 2010), although this correlation could be caused  
138 by differential responses to decadal-scale ecosystem transitions (Beamish 1995) and/or reflect  
139 differing trophic dynamics between the two species (van der Lingen et al. 2006). Further research  
140 based on additional time-series data and biological information is, however, required to support  
141 the competition hypothesis. Other potential competitors that share some common prey items  
142 and habitat with Pacific Herring include Pink (*O. gorbuscha*), Chum (*O. keta*), and Sockeye (*O.*  
143 *nerka*) Salmon (Haegele 1997, Beamish et al. 2004).

144           Additional abiotic and biotic conditions are also thought to affect Pacific Herring  
145 recruitment and biomass, although different studies have yielded conflicting results, with  
146 biological mechanisms not being fully resolved (Tester 1948, Stocker & Noakes 1988, Zebdi &  
147 Collie 1995, Williams & Quinn II 2000, Ware & Thomson 2005, Perry & Schweigert 2008). For  
148 instance, Tester (1948) found that warm years have a detrimental effect on Pacific Herring  
149 biomass off the WCVI. Schweigert (1995) found an inverse correlation between Pacific Herring  
150 biomass and July sea surface temperature (SST) off the WCVI during 1935-1988. Similarly,  
151 McFarlane et al. (1997) found that Pacific Herring biomass was negatively related to SST and  
152 argued that this temperature effect could be mediated by Pacific Hake migration into BC waters  
153 and the resultant added predation pressure. Conversely, Zebdi & Collie (1995) suggested that  
154 warm and wet winters could favour future Pacific Herring recruitment, while Stocker & Noakes  
155 (1988) found a positive association between salinity, SST, and high recruitment estimates  
156 between 1950 and 1980 in BC. A significant positive linear relationship between Pacific Herring  
157 carrying capacity and primary productivity in the northeastern Pacific and eastern Bering Sea  
158 during the second half of the 20<sup>th</sup> century was found by Perry & Schweigert (2008), suggesting

159 possible bottom-up control of Pacific Herring biomass. Similarly, Ware & Thomson (2005) found  
160 a strong positive relationship between primary productivity and resident fish (including Pacific  
161 Herring) populations on the western coasts of North America.

162 Pacific Herring stock assessments (e.g., Schweigert & Haist 2007; DFO 2018), the design  
163 of harvest control rules (Cleary et al. 2010), as well as the calibration of individual-based models  
164 that aim to infer trophic relationships and drivers of stock fluctuations (e.g., Fu et al. 2017) rely  
165 on estimates of Pacific Herring biomass (i.e. 'biomass indices') in different stock areas of BC. In  
166 BC, Pacific Herring egg deposition (spawn) surveys are used to back-calculate the biomass of  
167 mature spawners; however, there is no explicit statistical treatment of spatio-temporal  
168 autocorrelation in estimates of spawner biomass. In addition, and given the estimated increase  
169 in natural mortality of WCVI Pacific Herring in recent years (DFO 2018), there is a need to  
170 understand factors affecting adult Pacific Herring during the summer foraging period. In the  
171 scientific community, there has been a growing interest in the calibration of dynamic species  
172 distribution models that explicitly account for spatial and/or temporal patterns in fish biomass,  
173 which are partly driven by 'latent' unmeasured variables (Shelton et al. 2014, Thorson, Skaug, et  
174 al. 2015, Thorson 2015, Thorson et al. 2017). Moreover, there is a growing body of evidence  
175 suggesting that simultaneously modelling the distribution of several species occurring in the  
176 same ecosystem (commonly referred as to 'joint species distribution models'; Ovaskainen et al.  
177 2017) can improve estimates of individual species abundance indices in cases where spatial  
178 distribution patterns of one species can provide a good proxy for another (Hui et al. 2015,  
179 Thorson, Scheuerell, et al. 2015, Warton et al. 2015, Ovaskainen et al. 2016, Thorson et al. 2016).  
180 Between-species covariation can be further measured from joint species distribution models,  
181 which provide valuable information when inferring trophic relationships or competitive  
182 interactions (Thorson, Scheuerell, et al. 2015, Thorson et al. 2016).

183 The goal of this study was to improve understanding of the spatio-temporal dynamics of  
184 Pacific Herring off the WCVI, over the period 2006-2014. We quantified covariation with demersal  
185 and pelagic species, and tested whether there are strong environmental and/or biological  
186 correlates of Pacific Herring density. Spatio-temporal vector autoregressive models were fit to:  
187 (i) describe spatio-temporal fluctuations of Pacific Herring distribution off the WCVI; (ii) estimate

188 the dynamics of Pacific Herring abundance through time; (iii) quantify the effects of abiotic and  
189 biotic factors on Pacific Herring distribution; and (iv) investigate spatio-temporal covariation with  
190 prey species as well as potential predators and competitors, which can, in turn, be informative  
191 about causes of Pacific Herring natural mortality and trophic ecosystem dynamics.

## 192 **MATERIALS AND METHODS**

### 193 ***Overview***

194 We analyzed three fishery independent data sets, to represent Pacific Herring and their potential  
195 predators and competitors. The first of these was a pelagic near-surface trawl survey conducted  
196 at night; the second was a multispecies bottom trawl survey conducted during the day; and the  
197 third was an acoustic survey targeting Pacific Hake. We interpreted these datasets as showing  
198 covariation between Pacific Herring and potential predators and competitors. When analyzing  
199 these data, we also accounted for zooplankton and physical ocean conditions (see below for  
200 details), and used the overlap between these data sets to infer physical and biological drivers of  
201 Pacific Herring distribution and density.

### 202 ***Data Sources***

#### 203 ***Pelagic fish***

204 DFO's night trawl survey targeting pelagic (i.e. in the water column) fish species was conducted  
205 annually between 2006 and 2014 (except in 2007) off the WCVI, aboard the Canadian Coast  
206 Guard Ship, W.E. Ricker (no surveys were conducted after 2014). This survey was designed to  
207 estimate Pacific Sardine abundance, but also provides abundance estimates for Pacific Herring,  
208 and for Chinook, Chum, Coho, Pink and Sockeye Salmon. The survey was conducted in late July-  
209 early August and stations were randomly selected, based on a 10 km x 10 km grid, prior to the  
210 survey within a pre-defined core area (Flostrand et al. 2011, 2015) (Appendix S1A). Sampling was  
211 conducted using a 250/350/14 midwater rope trawl (Cantrawl Pacific Ltd., Richmond, B.C.), with  
212 1,100 kg U.S.A. Jet doors, towed near the surface (< 30 m deep) at about 5 knots for up to 30  
213 minutes (Flostrand et al. 2011). Catches were identified to species and weighed. Catch-per-unit-  
214 effort (CPUE) was calculated by dividing catch weight by volume swept, which was estimated as

215 the product of the net mouth opening width, height, and distance towed (Flostrand et al. 2011).  
216 The minimum and maximum numbers of sampling stations were 45 and 109, in 2006 and 2009  
217 respectively (Appendix S1A). The average number of stations sampled per year was 75.

### 218 ***Groundfish***

219 Data were compiled from DFO's synoptic bottom trawl groundfish surveys, which were  
220 conducted biennially between 2006 and 2014, aboard the R/V W.E. Ricker. These surveys are  
221 typically used to provide long-term biomass estimates for demersal fish species off the WCVI  
222 (Workman et al. 2008). We focused on seven species thought to be main predators of Pacific  
223 Herring, namely Pacific Hake, Lingcod, Pacific Cod, Arrowtooth Flounder, Sablefish, North Pacific  
224 Spiny Dogfish (*Squalus suckleyi*), and Pacific Halibut. This survey was conducted in June and  
225 followed a random, depth-stratified design with 2 km X 2 km sampling units (Workman et al.  
226 2008) (Appendix S1B). Fish were sampled during the day, using an Atlantic Western IIA box trawl  
227 with 1,100 kg U.S.A. Jet doors. Fish were sorted to species and weighed. CPUE was estimated by  
228 dividing catch weight by area swept, which was calculated as the product of doorspread and  
229 distance towed. When doorspread measurements were lacking, annual average doorspread  
230 values were used. The minimum and maximum numbers of sampling localities were 144 and 172,  
231 in 2010 and 2008 respectively. The average number of sampling localities per individual survey  
232 was 161.

### 233 ***Pacific Hake***

234 We compiled data from DFO's and NOAA's joint Pacific Hake acoustic-trawl survey, which is  
235 conducted on an annual or biennial basis (2009, 2011, 2012 and 2013 for the purpose of this  
236 study) for the area off of the WCVI. These surveys were conducted in August and September, and  
237 involved collecting acoustic data along parallel transects spaced 10 or 20 nautical miles apart off  
238 WCVI (Appendix S1C). Acoustic signals attributable to Pacific Hake were verified and sampled  
239 using midwater trawls. A full description of the survey as well as methods used to derive  
240 estimates of Pacific Hake biomass was provided by Edwards et al. (2018).

### 241 ***Zooplankton***

242 Zooplankton biomass data were collected during the pelagic night trawl survey from 2009-2014.  
243 Zooplankton species were sampled by conducting vertical net hauls from a maximum of 250 m  
244 depth (or within 5 m of the bottom) to the surface. A black bongo net frame (0.25 m<sup>2</sup> mouth  
245 area) was fitted with a TSK flowmeter and two 0.23 mm black nylon mesh nets (Mackas et al.  
246 2001, Galbraith et al. 2016). All zooplankton were identified to the highest possible taxonomic  
247 resolution and life history stage, and then counted. Species counts were multiplied by their  
248 average dry weight, as estimated from laboratory and literature analyses. An index of  
249 zooplankton density (mg/m<sup>3</sup>) was derived for each sampling locality by dividing species weights  
250 by volume filtered (as estimated from the flowmeter). From these data, we estimated for each  
251 sampling locality: the total density of all recorded zooplankton species belonging to the Order  
252 Euphausiacea (collectively referred to as Euphausiids in the following text); and the total density  
253 of 40 zooplankton taxa (of several sizes and stages) known to be prey of Pacific Herring (referred  
254 to as total prey density; J. Boldt, DFO, unpublished data – see Appendix S2).

### 255 ***Environmental covariates***

256 A total of 13 environmental and lower trophic level descriptors hypothesized to affect Pacific  
257 Herring distribution or abundance were acquired from two sources (Table 1): 1) Aqua Moderate  
258 Resolution Imaging SpectroRadiometer (MODIS) satellite data (Salomonson et al. 1989) ; and 2)  
259 data from vertical casts conducted during surveys using sensors mounted on a conductivity,  
260 temperature, and depth recorder (CTD). We used monthly satellite-based estimates of  
261 chlorophyll *a* concentration (mg/m<sup>3</sup>) produced by MODIS for the months of April, May, June and  
262 July as an indicator of spring and summer phytoplankton standing stock that could enhance  
263 zooplankton productivity, a prey resource for Pacific Herring in the spring and summer (Ware &  
264 Thomson 2005, Perry & Schweigert 2008). We also downloaded sea surface temperatures (SST;  
265 degrees Celsius) for those months when Pacific Herring would be foraging in the study area.  
266 MODIS data were downloaded at a resolution of 4X4 km and rasterized. We then extracted the  
267 value of descriptors for each combination of fish-sampling locality and year. To derive a yearly  
268 shelf-wide index of seasonal temperature off the WCVI, we calculated the mean of monthly

269 MODIS-derived temperature values within the minimum convex polygon encompassing pelagic  
270 night trawl survey sampling localities for each year (Appendix S3).

271 Data collected using CTD sensors included water temperature (degrees Celsius), salinity (practical  
272 salinity units - psu), oxygen content (mL/L), fluorescence (mg/m<sup>3</sup>), and transmissivity (%/m),  
273 which could serve as proxies of phytoplankton standing stock and/or reflect metabolic  
274 constraints for Pacific Herring. Previous studies have linked salinity to Pacific Herring recruitment  
275 (Stocker and Noakes 1988) and oxygen content has been linked to the distribution of other fish  
276 species (Keller et al. 2015). Fluorescence and transmissivity may help elucidate changes in  
277 phytoplankton standing stock and, therefore, zooplankton and prey availability. Temperature  
278 and salinity data were collected during the pelagic night trawl survey. As fluorescence, oxygen  
279 and transmissivity were not recorded for all pelagic night trawl surveys, additional information  
280 about these three descriptors was collected from other DFO oceanographic surveys conducted  
281 annually in late spring (e.g. between May 15<sup>th</sup> and June 15<sup>th</sup>). Data used in spatio-temporal  
282 models were from CTD samples obtained in water at a pressure of *ca.* 10 dBar (approximately 10  
283 m depth). We chose 10 m because this was the depth with a maximum number of available  
284 samples. In addition, data collected at 10 m depth provide a possibly interesting complement to  
285 sea surface temperature and chlorophyll data collected via satellite images. Each fish-sampling  
286 locality was assigned a CTD-based environmental dataset extracted from the nearest CTD  
287 sampling locality in a given year.

288

### 289 ***Modelling approach***

290 We fit single-species and multi-species spatial dynamic factor analyses (referred here to as Vector  
291 Autoregressive Spatio-Temporal, *VAST*, models) developed by Thorson, Scheuerell, et al. (2015)  
292 and Thorson et al. (2016), which are convenient and flexible variants of the classical delta-models  
293 (Lo et al. 1992, Stefánsson 1996) that can explicitly address spatio-temporal autocorrelation in  
294 fish biomass. All computations were performed using TMB package (Kristensen et al. 2016) in the  
295 R language for statistical computing (R Core Team 2018). The statistical framework of *VAST* is  
296 exhaustively described elsewhere (see Thorson, Scheuerell, et al. 2015, Thorson et al. 2016,

297 Thorson & Barnett 2017), and we present only a brief overview of the modelling approach. A  
298 detailed history and description of *VAST* is also available in Thorson (2019).

299 The *VAST* model estimates one or more ‘factors’, which account for spatial autocorrelation in  
300 fish distribution data and reflect potential latent environmental and/or biological variables  
301 driving species distribution (Thorson, Scheuerell, et al. 2015). Each factor is estimated as a  
302 Gaussian Markov random field, reflecting the assumption that fish abundances in nearby  
303 sampling locations are typically more similar than in distant ones (Thorson, Scheuerell, et al.  
304 2015). The *VAST* model can address both spatial patterns that are constant through time (‘spatial  
305 variation’), and spatial patterns that vary through time (‘spatio-temporal variation’) (Thorson et  
306 al. 2016). It can therefore be used to describe the realized niche of species as well as their  
307 response to variation in local environmental conditions. This flexible modelling framework also  
308 allows the incorporation of environmental covariates as fixed effects (Thorson 2015, Thorson et  
309 al. 2017). Fixed effects are estimated via a maximum marginal likelihood while integrating across  
310 all random effects. The Laplace approximation is used to approximate the marginal likelihood  
311 (Skaug & Fournier 2006) and then the fixed effects are estimated values maximizing the marginal  
312 likelihood function using a non-linear optimizer (Kristensen et al. 2016). Parameter estimation  
313 can become computationally unfeasible as the number of sampling localities and species  
314 increase. To avoid computational issues, a mesh of ‘knots’ is usually pre-defined by the user and  
315 serves to approximate random fields over the domain under study (Thorson, Shelton, et al. 2015).  
316 The location of knots is calculated using a k-means cluster algorithm and the value of the random  
317 field is assumed to be piecewise constant at every knot. When calculating total fish abundance  
318 over the entire sampling domain and/or derived quantities (e.g., abundance index), the knots are  
319 weighted by their area to avoid bias in estimates caused by differences in sampling intensity  
320 among different areas of the spatial domain (Thorson, Shelton, et al. 2015).

321 We fit the recently developed “Poisson-link” delta-model developed by Thorson (2017),  
322 which estimates the catch number density (first model component) and average catch weight  
323 (second model component) for every combination of year and sampling locality using log-linked  
324 linear predictors, and is thus similar to a compound Poisson-gamma approach (Thorson 2017).

325 Both components of the Poisson-link delta-model are approximated using a linear predictor:

326 (1) First model component (catch number density):

$$\begin{aligned}
 327 \quad p_1(i) = & \underbrace{\beta_1(c_i, t_i)}_{\text{Intercepts}} + \underbrace{\sum_{f=1}^{n\omega_1} L_{\omega_1}(c_i, f)\omega_1(s_i, f)}_{\text{Spatial term}} + \underbrace{\sum_{f=1}^{n\varepsilon_1} L_{\varepsilon_1}(c_i, f)\varepsilon_1(s_i, f, t_i)}_{\text{Spatio-temporal term}} \\
 328 \quad & + \underbrace{\sum_{p=1}^{n_p} \gamma_1(c_i, p, t_i)x(s_i, p, t_i)}_{\text{Covariate effect}}
 \end{aligned}$$

329 (2) Second model component (average catch weight):

$$\begin{aligned}
 330 \quad p_2(i) = & \underbrace{\beta_2(c_i, t_i)}_{\text{Intercepts}} + \underbrace{\sum_{f=1}^{n\omega_2} L_{\omega_2}(c_i, f)\omega_2(s_i, f)}_{\text{Spatial term}} + \underbrace{\sum_{f=1}^{n\varepsilon_2} L_{\varepsilon_2}(c_i, f)\varepsilon_2(s_i, f, t_i)}_{\text{Spatio-temporal term}} \\
 331 \quad & + \underbrace{\sum_{p=1}^{n_p} \gamma_2(c_i, p, t_i)x(s_i, p, t_i)}_{\text{Covariate effect}}
 \end{aligned}$$

332 In these equations,  $p_1(i)$  and  $p_2(i)$  represent the predictors for observation  $i$ ,  $\beta_1(c_i, t_i)$  and  
 333  $\beta_2(c_i, t_i)$  are the intercepts for species  $c_i$  and year  $t_i$ ;  $\omega_1(s_i, f)$  and  $\omega_2(s_i, f)$  represent spatial  
 334 variation at location  $s_i$  for factor  $f$ ;  $L_{\omega_1}(c_i, f)$  and  $L_{\omega_2}(c_i, f)$  are the loadings matrices that  
 335 generate spatial covariation among categories  $c_i$  for the linear predictors;  $\varepsilon_1(s_i, f, t_i)$  and  $\varepsilon_2(s_i, f,$   
 336  $t_i)$  represent spatio-temporal variation at location  $s_i$  for factor  $f$  at time  $t_i$ ;  $L_{\varepsilon_1}(c_i, f)$  and  $L_{\varepsilon_2}(c_i, f)$   
 337 are the loadings matrices that generate spatio-temporal covariation for the predictors;  $x(s_i, p, t_i)$   
 338 are measured values at location  $s_i$  for environmental covariate  $p$  at time  $t_i$  that explain variation  
 339 in fish density and  $\gamma_1(c_i, p, t_i)$  and  $\gamma_2(c_i, p, t_i)$  are the estimated impacts of those  
 340 environmental covariates.

341

342 **Effects of physical and biological covariates on Pacific Herring dynamics**

343 We aimed to investigate the effects of physical and biological covariates on Pacific Herring spatio-  
344 temporal patterns off the WCVI. To achieve this goal, we used a forward stepwise modelling  
345 approach based on a set of the covariates listed in Table 1 (this approach is referred to as Model  
346 #1; Table 2). A total of 26 single-species models were fitted to Pacific Herring data only, each  
347 model accounting for an individual linear or quadratic covariate effect on both components of  
348 the model. We compared these models to a null model (i.e., a model with no covariates) and  
349 selected the best model based on the Akaike Information Criterion (AIC) (Akaike 1974) (i.e., the  
350 model with the lowest AIC value). We then included each remaining individual covariate in the  
351 previously selected model, selected the best model again and repeated this process until no  
352 added covariate improved the AIC of models. When a SST or chlorophyll covariate was selected  
353 during the stepwise procedure, we then removed all SST or chlorophyll descriptors respectively,  
354 to avoid potential issues arising from including collinear covariates. In these models, we used as  
355 many knots as there were unique fish-sampling locations (Table 2). We did not inform the model  
356 with a user-predefined spatial grid, meaning that the spatial domain used when calculating  
357 derived quantities (e.g., abundance indices) was directly inferred from the location of samples.  
358 We divided the abundance indices by their mean to get a relative index of abundance. To reduce  
359 computational time, no bias-correction method was implemented in any of these models  
360 (Thorson & Kristensen 2016). A summary of *VAST* parameters for the model #1 is provided in  
361 Table 2.

### 362 **Calibration of multi-species *VAST* models and derivation of biomass index**

363 A summary of the different fitted models including data sources, data sample size for each  
364 survey, time-coverage and *VAST* parameters is provided in Appendices S1a, S1b, S1c and Table 2.  
365 Before calibrating the multi-species models, we fit a single-species model for Pacific Hake over  
366 the period 2009-2013 using the *VAST* parameters listed in Table 2 (referred to as Model #2 in the  
367 following text).

368 Since not all datasets have exactly the same time-coverage, we independently fit several  
369 multi-species models to address covariation between Pacific Herring and zooplankton and  
370 potential pelagic predators/competitors. We fit four multi-species models: (i) a model accounting

371 for Pacific Herring and bottom-associated and semi-pelagic predators, including Pacific Hake,  
372 Arrowtooth Flounder, Pacific Halibut, Lingcod, Pacific Cod, North Pacific Spiny Dogfish, and  
373 Sablefish using bottom-trawl samples for the period 2006-2014 (referred to as Model #3; Table  
374 2); (ii) a model accounting for Pacific Herring and some of their potential pelagic competitor  
375 species (Pacific Sardine, Chum Salmon, Sockeye Salmon, and Pink Salmon) and predator species  
376 (Coho Salmon and Chinook Salmon) using pelagic-trawl samples for the period 2006-2014  
377 (referred to as Model #4; Table 2); (iii) a model accounting for Pacific Herring, acoustics-based  
378 Pacific Hake data, total prey density of Pacific Herring (i.e., zooplankton species known as prey of  
379 Pacific Herring based on stomach content data) and Euphausiids for the period 2009-2013  
380 (referred to as Model #5; Table 2); and (iv) a model accounting for Pacific Herring and total prey  
381 density of Pacific Herring for the period 2009-2014 (referred to as Model #6; Table 2). In multi-  
382 species models, we fixed the intercepts as constant over time so that spatio-temporal covariation  
383 among species could be interpreted as inter-annual trends in abundance (Table 2). We chose a  
384 principal component analysis approach to rotate the spatial factors and loading matrix (“PCA-  
385 rotation”), which simplified the interpretation of spatial factors (Thorson et al. 2016). For each  
386 model component, we calculated the proportion of variance that is explained by each factor (i.e.,  
387 by dividing the eigenvalues associated with each factor by the sum of eigenvalues of all factors).  
388 We estimated correlations in spatio-temporal densities among species and tested their  
389 significance via a Wald test i.e., the ratio (estimate of correlation: standard error) is compared to  
390 a standard normal distribution, the null hypothesis being that the true correlation is zero (level  
391 of significance: 0.05) (Davidson et al. 2004). We calculated the proportion of total variance that  
392 is explained by each spatial ( $\omega_1$  and  $\omega_2$ ) and spatio-temporal component ( $\epsilon_1$ ,  $\epsilon_2$ ) of the delta-  
393 model by dividing the sum of eigenvalues of the covariance matrix of each model component by  
394 the sum of all eigenvalue of four covariance matrices; this interpretation is justified given that all  
395 components act additively for predicting log-density of each species.

396 In the following, we interpret correlation among species in multispecies *VAST* models as  
397 follows.

398 1. We infer that a negative and significant correlation between herring and a known

399 predator indicates either a direct (consumption) or indirect (behavioral avoidance) impact  
400 of predator upon herring;

401 2. We infer that a negative and significant correlation between herring and known  
402 competitors implies either evidence of competition;

403 3. We infer that a positive and significant correlation between herring and a known predator  
404 may reflect either predation (i.e., the abundance of the predator is driven by the  
405 availability of Herring), or shared responses to environmental variation and prey  
406 availability

407 We acknowledge that these interpretations are subject to several potential caveats including:

408 A. Data are observational, and therefore causal interpretation is not always justified. We  
409 therefore warrant that our interpretations are hypotheses, which were confronted to  
410 existing knowledge on WCVI ecosystem, and note below where future research could  
411 support or discredit these hypotheses;

412 B. By necessity, there are differences in the seasonal timing of surveys, potentially raising  
413 concerns that some patterns may arise due to differences in seasonal movement among  
414 species. We note instances where this concern is justified, while also noting when we  
415 have evidence that species inhabit a consistent spatial distribution over the periods  
416 analyzed (April-Sept) such that these concerns about seasonal variation are not  
417 warranted.

418 C. The spatial scale of this study is small relative to population dynamics for transboundary  
419 species, such as Pacific Hake. We therefore include data and phrase conclusions for  
420 Pacific Hake as applying to the portion of the coastwide stock abundance that is  
421 distributed in Canadian waters during summer months.

422

423 **RESULTS**

424 **Spatio-temporal dynamics of Pacific Herring biomass off the WCVI (model #1)**

425 The geographic range of Pacific Herring encompassed most of the WCVI study area except the  
426 furthest offshore areas sampled (Fig. 1a). The single-species spatio-temporal model (Model #1)  
427 showed an overall increase in the VAST-derived relative abundance index for Pacific Herring in  
428 the summer pelagic survey off the WCVI during 2006-2014 (Fig. 1). The lowest relative abundance  
429 indexes were found during 2006-2009, after which abundance increased, particularly after 2012  
430 (Fig. 1). Hotspots of Pacific Herring density occurred in south-western areas in 2010-2014 (e.g. La  
431 Perouse bank area) as well as in northwestern areas beginning in 2011 (Fig. 1).

432

### 433 **Effects of environmental covariates on Pacific Herring (model #1)**

434 The highest gain in model parsimony was obtained when adding the May estimate of MODIS-  
435 derived SST in the model ( $\Delta AIC \approx 5$ ). The model estimated a quadratic relationship between  
436 variation in Pacific Herring biomass and May SST (Fig. 2). Accounting for the water oxygen content  
437 also improved model parsimony even though the gain in AIC was lower ( $\Delta AIC \approx 0.2$ ) and the  
438 graphical representation of the relationships between this variable and the predicted biomass  
439 did not yield an easily interpretable pattern (data not shown).

440

### 441 **Spatio-temporal covariation between Pacific Herring and other fish species**

442

### 443 ***Multi-species VAST model with bottom-associated groundfish species (model #3)***

444 Variation in catch number-density (the first component of the delta-model) accounted for  
445 69.8% of the variance explained by the delta-model, while variation in average catch weight (the  
446 second component of the delta-model) explained the remainder. As variation in catch number-  
447 density explained most of the variance, we present only the spatial and spatio-temporal factor  
448 maps related to the first component.

449 *Spatial variation in catch number-density*

450 The first factor for spatial variation in catch numbers-density ( $\omega_1$ ) accounted for 25.12%  
451 of all variance explained by the delta-model. This reflects high catch rates for Pacific Herring and  
452 three other species (Lingcod, Pacific Cod and Pacific Halibut) in the southwestern areas of La  
453 Perouse, Swiftsure Banks, and northwestern inshore regions off the WCVI, as well as high catch  
454 rates for Sablefish and Pacific Hake along the shelf break and in the most offshore sampled areas  
455 (Fig. 3). The second factor for spatial variation in catch number-density explained 11.5% of all  
456 variance, and reflected high densities of Spiny Dogfish and Arrowtooth Flounder in most offshore  
457 areas off the WCVI as well as in the La Perouse Bank and northwestern inshore regions off the  
458 WCVI. Lingcod, Pacific Cod, North Pacific Spiny Dogfish and Pacific Halibut had a significant  
459 positive correlation with spatial variation in Pacific Herring catch number-density ( $\omega_1$ ) and with  
460 one another according to significance Wald tests (Fig. 4). Sablefish, Pacific Hake and Arrowtooth  
461 Flounder had significant negative correlation with spatial variation in Pacific Herring catch  
462 number-density ( $\omega_1$ ) and with one another (Fig. 4).

463

#### 464 *Spatio-temporal variation in catch number-density*

465 The first factor for spatio-temporal variation in catch number-density ( $\epsilon_1$ ) explained 13.6%  
466 of all variance explained by the delta-model. This factor represents hotspots for Pacific Herring,  
467 Pacific Cod, Sablefish and Arrowtooth Flounder in southern areas of WCVI including La Perouse  
468 bank in 2010, 2012 and 2014 (Fig. 5). An overall positive significant correlation with spatio-  
469 temporal variation in catch number-density was found between Pacific Herring, Sablefish,  
470 Lingcod, Pacific Halibut, Arrowtooth Flounder and Pacific Cod (Fig. 4). A significant negative  
471 correlation with spatio-temporal variation in catch number-density was found between Pacific  
472 Herring and two species, namely Pacific Hake and North Pacific Spiny Dogfish (Fig. 4).

473

#### 474 ***Multi-species VAST model with pelagic species (model #4)***

475 Variation in average catch weight (the 2<sup>nd</sup> component of the delta-model) accounted for  
476 55% of the variance explained by the delta-model, while variation in catch number-density

477 explained the remainder. The first factor for spatial variation in catch number-density explained  
478 18.5% of all variance explained by the delta-model. This factor represented high catch rates for  
479 all species in inshore regions, particularly in southern areas, off the WCVI (Fig. 6). The first factor  
480 for spatial variation in average catch weight was not associated with an easily interpretable  
481 biomass spatial pattern (Fig. 6). The second factor accounted for 2.9% of all explained variance  
482 and represented hotspots for Pacific Herring on La Perouse bank (Fig. 6). We found a significant  
483 positive correlation between Pacific Herring and all pelagic species for spatial variation in  
484 numbers-density and average catch weight (Fig. 7).

485         The first factor for spatio-temporal variation in numbers-density contributed to 10.6 % of  
486 all explained variance, and this factor represents high catch rates for all species, including Pacific  
487 Sardine and Pacific Herring, in offshore regions south-west of Vancouver Island in 2008 and 2009  
488 and inshore regions in the south-east in 2012 and 2014 (Fig. 8). Pacific Sardine and Pacific Herring  
489 yielded negative and positive scores respectively for the second factor for spatio-temporal  
490 variation in numbers-density (Fig. 8) that contributed to 4.4% of all explained variance. This factor  
491 mainly reflected zero catch rates for Pacific Sardine in 2013 and 2014 off the WCVI while Pacific  
492 Herring reached a peak in abundance during these years. We found a significant overall negative  
493 correlation between Pacific Herring and Pacific Sardine for spatio-temporal variation in numbers-  
494 density (Fig. 7).

495

#### 496 ***VAST model for Pacific Hake acoustic-derived data (models #2 and #5)***

497         The single-species VAST model (model #2) inferred a high relative abundance index for  
498 Pacific Hake off the WCVI in 2009 while lower abundances were predicted for the years 2011 and  
499 2013 (Appendix S4). For the model #5, variation in numbers-density (the first component of the  
500 delta-model) accounted for 84.2% of the variance explained by the multi-species delta-model,  
501 while variation in average catch weight (the second component of the delta-model) explained  
502 the remainder. We thus focused here on the first component of the model #5 that accounts for  
503 the majority of explained variance. Models inferred high catch rates for Pacific Hake in most  
504 offshore regions off WCVI during the period 2009-2013 and this pattern is constant through time

505 (Fig. 9a & 9b). We found a strong significant overall negative correlation between Pacific Herring  
506 and Pacific Hake for spatial variation in numbers-density (Fig. 9c). However, we found (i) a  
507 negative correlation between Pacific Herring and Euphausiids for spatial variation in numbers-  
508 density (Fig. 9c); (ii) an overall positive correlation between Pacific Herring and zooplankton prey  
509 of Pacific Herring for spatial variation in numbers-density (Fig. 9c); (iii) an overall negative  
510 correlation index between Pacific Herring and Pacific Hake for spatio-temporal variation in  
511 numbers-density (Fig. 9d); and (iv) a positive correlation between Pacific Herring and both  
512 Euphausiids and zooplankton prey species for spatio-temporal variation in numbers-density (Fig.  
513 9d). According to Wald tests, however, none of these correlations were significant.

514

#### 515 ***VAST model for Pacific Herring and zooplankton data (model #6)***

516 Spatial and spatio-temporal variation in numbers-density (the first component of the delta-  
517 model) accounted for 25.7% and 8.1% of the variance explained by the delta-model respectively,  
518 while spatial and spatio-temporal variation in average catch weight (the second component of  
519 the delta-model) explained 66.3% and <0.001% of the variance explained by the delta-model  
520 respectively. We found an overall positive correlation between Pacific Herring and zooplankton  
521 prey for spatial variation in numbers-density (correlation = 0.64, standard error = 0.51) and  
522 average catch weight (correlation = 0.23, standard error = 4.94), neither of which was significant  
523 according to Wald tests. We found an overall positive correlation between Pacific Herring and  
524 zooplankton prey for spatio-temporal variation in numbers-density, which was not significant  
525 according Wald tests (correlation = 0.58, standard error = 0.38). The evolution of the VAST-  
526 derived abundance index through time for Pacific Herring prey off the WCVI was characterized  
527 by an overall increase between 2009 and 2014 (Appendix S5).

528

#### 529 **DISCUSSION**

530 Drivers shaping Pacific Herring abundance and mortality have been analysed elsewhere  
531 (Schweigert 1995, McFarlane 1997, Tanasichuk 2000, Schweigert et al. 2010) but to our

532 knowledge, this is the first study that estimates spatio-temporal summer offshore dynamics of  
533 Pacific Herring using a statistical modelling approach that simultaneously accounts for spatio-  
534 temporal autocorrelation in fish biomass as well as spatio-temporal covariation with prey and  
535 potential predator or competitor fish species. The present study is unique in simultaneously  
536 analyzing a broad array of different datasets that had never before been assembled together.  
537 Unlike other previous studies (Schweigert 1995, McFarlane et al. 1997, Schweigert et al. 2010),  
538 we used spatio-temporal models to analyze these fisheries-independent catch time-series  
539 collected from multiple surveys, all of which were conducted with random-stratified sampling  
540 designs, which is necessary for deriving non-biased abundance estimates and between-species  
541 covariation estimates (Thorson, Shelton, et al. 2015).

542 In the present study, hotspots of Pacific Herring were consistently found in continental  
543 shelf waters with bottom depths of 43 – 185 m (i.e., 5<sup>th</sup> to 95<sup>th</sup> percentiles for positive Pacific  
544 Herring catch), while Pacific Herring were less frequent and abundant in waters along the shelf  
545 break, which were characterized by high densities of Euphausiids, Pacific Hake, Sablefish and  
546 Arrowtooth Flounder. We found that increases in Pacific Herring biomass off the WCVI during the  
547 period 2006-2014 were quadratically correlated with local increases of May SST. Models also  
548 found a negative correlation for variation in spatio-temporal densities between Pacific Herring  
549 and both Pacific Hake and Pacific Sardine, which could reflect fluctuations of natural mortality  
550 driven by predation and competitive interactions, respectively. Despite a lack of statistical  
551 significance, correlation for variation in spatio-temporal densities between Pacific Herring and its  
552 common prey species were positive, suggesting potential bottom-up control mechanisms.  
553 Finally, correlation for variation spatio-temporal densities between Pacific Herring and several of  
554 its predators (i.e., Arrowtooth Flounder, Sablefish, Pacific Halibut, Pacific Cod, Coho Salmon and  
555 Chinook Salmon), were positive, suggesting increases in densities of these species may not exert  
556 negative impact over herring abundance. For Arrowtooth Flounder and Sablefish, this pattern  
557 could be partly explained by the fact that both species had significant negative correlation with  
558 spatial variation in Pacific Herring density, which might reflect a low prey/predator spatial overlap  
559 and thus a moderate predation pressure from those predators. This finding highlights the need  
560 for further investigation of the relative contribution of those fish to the total summer offshore

561 predation experienced by Pacific Herring off the WCVI. These results are discussed in greater  
562 detail below.

563

#### 564 **Spatial patterns constant through time**

565 The *VAST* approach has the advantage of separating spatial patterns that are constant through  
566 time and spatial patterns that vary through time, reflecting inter-annual species' responses to  
567 variation in unobserved local environmental and/or biotic conditions. The typical mid-summer  
568 spatial distribution of Pacific Herring off the WCVI over the period 2006-2014 is similar to  
569 previously published observations i.e., hotspots usually tend to occur on the continental shelf  
570 (waters with bottom depths < 185m) including La Perouse and Swiftsure Banks while lower  
571 abundances are generally found along the shelf-break in waters deeper than 185 m (McFarlane  
572 et al. 1997). Model outputs presented here show this typical Pacific Herring distribution remains  
573 stable across years. Interestingly, Herring distribution did not perfectly match the hotspots of  
574 Euphausiids, an important Herring prey species (Robinson 2000, Tanasichuk 2002), suggesting  
575 that Pacific Herring tend to occur in sub-optimal Euphausiid foraging areas. Two non-exclusive  
576 hypotheses could explain this pattern. The first, presented by McFarlane et al. (1997) suggests  
577 that this typical summer spatial pattern might reflect a 'food-predation risk trade-off' for Pacific  
578 Herring, i.e., Pacific Herring preferentially occur at the margins of Euphausiid hotspots to avoid  
579 Pacific Hake predation. Previous studies have shown that the Euphausiid hotspots usually  
580 harbour high densities of Pacific Hake (Mackas et al. 1997, McFarlane et al. 1997), which is a  
581 migratory species that usually enters BC waters in spring (May/early June), and mainly feeds on  
582 Euphausiids and Pacific Herring off the WCVI (Tanasichuk et al. 1991). In the present study  
583 (Models #3 & #6), we found that the shelf-break regions harbour high densities of several  
584 predators such as Pacific Hake, Sablefish and Arrowtooth Flounder, which provides additional  
585 support to the 'food-predation risk trade-off' hypothesis). Secondly, we also found a positive, but  
586 not significant, correlation in spatial patterns between Pacific Herring and its common prey  
587 species (Models #5 and #6). Thus, the second hypothesis could be that the typical mid-summer  
588 distribution of Pacific Herring is shaped by dietary preferences (i.e., its distribution tends to

589 match the range of its preferred prey) in addition to predation avoidance. The ‘food-predation  
590 risk trade-off’ mechanism proposed by McFarlane (1997) is based on the hypothesis that all  
591 Euphausiids are equally suitable prey for Herring, which has not been demonstrated. Further  
592 work on the feeding behaviour of Pacific Herring is therefore needed to establish whether or not  
593 low abundances of Herring along the shelf-break primarily reflect predation avoidance or dietary  
594 preferences or a combination of both.

595 Both Sablefish and Arrowtooth Flounder had contrasting spatial distributions when compared to  
596 Pacific Herring. The highest contrast in spatial distribution was found for Sablefish that typically  
597 occurred along the continental shelf break, which could be driven by unexplained bottom ocean  
598 conditions or intensity and direction of currents (McFarlane & Beamish 1983, McFarlane 1997).  
599 In the present study, the typical distributions of Arrowtooth Flounder and Pacific Herring were  
600 different (i.e. overall negative correlation in spatial pattern) even though the magnitude of this  
601 difference was lower for Arrowtooth Flounder than for Sablefish (Fig. 5). This is consistent with  
602 previous DFO surveys (e.g., the small mesh survey targeting shrimp), during which Pacific Herring  
603 and Arrowtooth Flounder were caught together on the WCVI shelf area, suggesting the  
604 distributions of both species partly overlap on the shelf. Since Euphausiids constitute a  
605 substantial part of the diet of both Sablefish and Arrowtooth Flounder (Ware & McFarlane 1986,  
606 Yang & Livingston 1986, Spies et al. 2017), prey availability could also explain why those species  
607 preferentially occur along the shelf break in summer. Conversely, Pacific Cod, Pacific Halibut and  
608 Lingcod were, like Pacific Herring, distributed on the continental shelf at the margins of  
609 Euphausiid hotspots. This finding could also be explained by dietary preferences and/or prey  
610 availability since Euphausiids are thought to constitute a minor part of the diet of those three  
611 species, which primarily feed on fish, crabs and shrimps (Beaudreau & Essington 2007,  
612 Moukhametov et al. 2008, Urban 2012).

613

#### 614 **Which factors drive the spatio-temporal fluctuations of Pacific Herring biomass?**

615 *Spatio-temporal fluctuations of Pacific Herring over the period 2006-2014*

616 We identified an overall increase in Pacific Herring relative abundance off the WCVI from  
617 2006 to 2014, which accelerated during 2012-2014 (Fig. 1). These findings are consistent with  
618 stock assessment estimates of trends in spawning biomass for both the SOG and WCVI stocks,  
619 i.e., the spawning biomass of the SOG stock increased after 2010 (towards historic high levels),  
620 and the WCVI stock increased from 2012-2014, from historic low levels from 2006-2010 (DFO  
621 2018). Both the WCVI and SOG assessed stocks of Pacific Herring forage off the southwest coast  
622 of Vancouver Island during the summer (Taylor 1964, Cleary et al. 2017), thus our results are  
623 consistent with stock assessment outputs.

624

#### 625 *Covariation with predators*

626 Multi-species model #5 found a negative correlation in spatio-temporal biomass patterns  
627 between Pacific Hake and Pacific Herring, suggesting that increases in Pacific Hake biomass are  
628 associated with declines in Pacific Herring density off the WCVI. This negative correlation might  
629 reflect different responses to environmental conditions or prey availability, but is consistent with  
630 previously-published studies suggesting that Pacific Hake is a main predator species that  
631 substantially contributes to Pacific Herring mortality off the WCVI (Ware & McFarlane 1986,  
632 1995, Tanasichuk et al. 1991, McFarlane et al. 1997). For instance, McFarlane et al. (1997)  
633 attributed the reduction in Pacific Herring abundance during warmer years off the WCVI to a  
634 concomitant increase in Pacific Hake-associated predation pressure. Similarly, Ware & McFarlane  
635 (1986) claimed that Pacific Hake has presumably much more impact on Pacific Herring mortality  
636 than other predators such as Sablefish or Pacific Cod off the WCVI.

637 Besides Pacific Hake, published literature and analyses of stomach content data suggest  
638 that Pacific Herring usually experience predation from several other groundfish including  
639 Lingcod, Pacific Cod, Spiny Dogfish, Sablefish, Arrowtooth Flounder and Pacific Halibut (Ware &  
640 McFarlane 1986, Tanasichuk et al. 1991, Beaudreau & Essington 2007, Brodeur et al. 2009) and  
641 some pelagic species (i.e., Coho Salmon and Chinook Salmon). However, the relative contribution  
642 of those species to total summer predation pressure experienced by Pacific Herring is not fully  
643 understood. In the present study, North Pacific Spiny Dogfish was the only bottom-associated

644 species that showed a negative correlation in spatio-temporal density with Pacific Herring. This  
645 negative correlation is not surprising as the distributions of Pacific Herring and Spiny Dogfish  
646 overlap on the WCVI shelf area and Pacific Herring constitutes an important part of the diet of  
647 Spiny Dogfish according to analyses of stomach content data (Jones & Geen 1977, DFO 1992,  
648 Brodeur et al. 2009). However, the negative correlation between Herring and North Pacific Spiny  
649 Dogfish was relatively weak (i.e. close to zero). Besides Pacific Hake and Spiny Dogfish, the  
650 present study did not identify any of other groundfish species as having a strong negative  
651 covariation in spatio-temporal densities with Pacific Herring. Indeed, models inferred a positive  
652 correlation of inter-annual trends in densities between Pacific Herring and Pacific Cod, Sablefish,  
653 Arrowtooth Flounder, Pacific Halibut and Lingcod. For Pacific Cod, this finding is similar to  
654 previous observations and might support the hypothesis of Ware & McFarlane (1986) claiming  
655 that this species does not have an important influence on Herring natural mortality off the WCVI  
656 and that the impact of this predator may have been previously overestimated. This hypothesis is  
657 also consistent with several analyses of stomach content data suggesting that Pacific Herring  
658 does not dominate the diet of Pacific Cod in the Gulf of Alaska (Jewett 1978, Albers & Anderson  
659 1985, Yang & Livingston 1986, Brodeur & Livingston 1988, Urban 2012), although other studies  
660 present contrasting results (Westrheim & Harling 1983, Tinus 2012). Analyses of stomach  
661 contents data in the Gulf of Alaska suggest that Pacific Herring does not dominate the diets of  
662 Arrowtooth Flounder, Sablefish or Pacific Halibut (Best & St-Pierre 1986, Brodeur & Livingston  
663 1988, Knoth & Foy 2008), which could explain the lack of negative spatio-temporal covariation of  
664 those predators with Pacific Herring. In addition, both Sablefish and Arrowtooth Flounder  
665 showed typical spatial distributions different from the range of Pacific Herring (i.e., negative  
666 correlation in spatial patterns - Fig. 5), which could reflect a lack of availability of Pacific Herring  
667 for those predators. It is, however, important to note that bottom trawl sampling may not  
668 perfectly depict the distribution of some predators, such as Sablefish or Dogfish, which are known  
669 to move throughout the column water and do not always occur near the bottom (Orlov et al.  
670 2011). Similarly, we did not find any negative impact of salmon on spatio-temporal densities of  
671 Pacific Herring, which could reflect that these species have a low relative contribution in the total

672 predation pressure. For those salmonids, it is also important to note that these species are  
673 migratory within the sampling area, which could constitute a source of uncertainty in catch data.

674 Overall the results of this study provide additional support to Ware & McFarlane's (1986)  
675 hypothesis that Pacific Herring may be more negatively impacted by Pacific Hake than other fish  
676 predators off the WCVI. Positive correlations between Pacific Herring and their predators may  
677 reflect convergent responses to environmental conditions and/or prey availability. A better  
678 understanding of seasonal and inter-annual variation in the feeding behaviours of predators is,  
679 therefore, required to address the relative contribution of each of those species in total predation  
680 pressure experienced by Pacific Herring. Further work is also needed to estimate absolute values  
681 of consumption of Pacific Herring (in weight) off the WCVI, which likely depend on a variety of  
682 interacting factors such as physical ocean conditions, densities of predators, overlap with  
683 predators and prey, and predator feeding behaviours. Finally, it is important to note that  
684 information on spatio-temporal dynamics as well as feeding behaviours of marine mammals (e.g.,  
685 Humpback Whales, Northern Fur Seals, Harbour Seals, California Sea Lions and Steller Sea Lions)  
686 should be included in further research as their impact on Pacific Herring mortality is thought to  
687 have increased during the last decades (Schweigert et al. 2010).

688

#### 689 *Covariation with potential competitors*

690 We fit a multi-species model (Model #4), based on pelagic night survey data to investigate  
691 covariation in spatio-temporal densities between Pacific Herring and its main pelagic competitors  
692 (i.e., Pacific Sardine, Pink, Chum and Sockeye Salmon; Haegele 1997, Beamish et al. 2004). No  
693 negative correlations in spatio-temporal densities were observed between Pacific Herring and  
694 the salmon species, suggesting that these salmon species do not have a substantial negative  
695 impact on Pacific Herring in offshore summer foraging grounds. However, we found a negative  
696 correlation in spatio-temporal densities between Pacific Sardine and Pacific Herring, which could  
697 reflect competitive interactions. Competition between these two species is likely since both  
698 species are opportunistic foragers and they have some zooplankton prey overlap (Boldt  
699 unpublished data, McFarlane et al. 2010). In addition, a negative association between both

700 species has previously been observed in WCVI waters (Schweigert 1995, Schweigert et al. 2010).  
701 In particular, it is intriguing that the recent peaks of Pacific Herring abundance occurred in 2013  
702 and 2014 when no Pacific Sardine were caught off the WCVI. We suggest that these results  
703 provide new evidence for a potential important negative association between Pacific Herring and  
704 Pacific Sardine off the WCVI. This should nevertheless be confirmed with further research.

705

#### 706 *Impact of ocean physical conditions and resource availability on Pacific Herring density*

707 The evolution of both VAST-derived abundance indexes for Pacific Herring and their prey  
708 (Appendix S5) off the WCVI showed very similar trends (i.e., an overall increase between 2009  
709 and 2014) suggesting that the spatio-temporal dynamics of Pacific Herring off the WCVI was  
710 partly driven by bottom-up factors. In addition, the models found a positive, but not significant,  
711 correlation between local resource availability (i.e., density of Pacific Herring prey) and Pacific  
712 Herring density, which further supports bottom-up drivers.

713 Positive anomalies in water temperatures are usually speculated to cause an increase in  
714 Pacific Herring natural mortality mediated by a decrease in resource availability (Robinson &  
715 Ware 1994) and/or prey composition (e.g. smaller and less lipid-rich zooplankton species, which  
716 are presumably of poorer quality for Pacific Herring, are usually more abundant during warm  
717 years off the WCVI; Galbraith & Young 2017). In the present study, we found a quadratic  
718 relationship between May SST and biomass of Pacific Herring, suggesting that extreme spring  
719 SSTs could have a negative impact on Herring biomass. We did not observe an overall decrease  
720 in Herring prey density during the warmest years of the time series, which could explain why  
721 increases in SST were not found as exerting a negative impact on Herring biomass. For instance,  
722 we found that the peak of prey availability off the WCVI occurred during the period 2012-2014  
723 (Appendix S5), which was one of the warmest periods off the WCVI during 2006-2014, according  
724 to shelf-wide MODIS-based SST indices (Appendix S3). Therefore, the observed positive  
725 association between some SST covariates and Pacific Herring density could be more indicative of  
726 a bottom-up effects of prey availability rather than a direct effect of water temperature, although  
727 the availability of lipid-rich vs. lipid-poor prey species was not explicitly examined in this study.

728 Similarly, the observed relationship between SST and Pacific Herring biomass could primarily  
729 reflect previously-discussed biotic interactions, such as peak Herring densities occurring during a  
730 period of very low abundances of Pacific Sardine off the WCVI (2012-2014).

731         There is a large body of evidence showing that positive anomalies in spring and/or  
732 summer water temperatures in the northeast Pacific enhance Hake migration into Canadian  
733 waters (Smith et al. 1990, Dorn 1995, McFarlane et al. 1997), and thus presumably negatively  
734 affect Herring stocks. In the present study, there was no strong evidence for a positive  
735 relationship between May SST and Pacific Hake biomass over the period 2009-2013. For instance,  
736 models suggested that high Hake densities occurred in 2009 off the WCVI, which was not one of  
737 the warmest years according to shelf-wide SST indices (Appendixes S3 & S5). Also, *VAST*-derived  
738 estimates of Hake biomass were low for 2013, which was one of the warmest years over this  
739 period based on shelf-wide May SST indices. The lack of positive correlation between SST and  
740 Hake biomass could then also partly explain why SST was not identified in the stepwise procedure  
741 as having a negative impact on Pacific Herring density. As suggested above for zooplankton, it is  
742 possible that the positive effect of SST found in our models reflects Hake predation rather than a  
743 direct effect of water temperature. We note, however, that there was higher uncertainty in  
744 Pacific Hake acoustics-derived biomass estimates in 2009 than in other years because of the  
745 presence of large populations of Humboldt squid during the acoustics survey (Stewart et al. 2011)  
746 and these results thus should be guardedly interpreted. Moreover, we note that a weakness of  
747 the present study is the limited number of overlapping years between the acoustics-based Hake  
748 survey and the pelagic survey, which precludes explicit testing of the Hake predation-mediated  
749 effect of SST on Herring natural mortality.

750         In summary, although correlative in nature, spatio-temporal model results suggest that  
751 the strongest drivers of Pacific Herring summer distribution and biomass are: i) zooplankton prey  
752 availability; ii) predator avoidance, particularly Pacific Hake; and iii) competition with sardines.  
753 Given the large body of non-exclusive hypotheses on the drivers shaping Pacific Herring natural  
754 mortality and stock fluctuations, we suggest follow up to this work should focus on disentangling  
755 the individual relative effects of ocean physical conditions, prey availability, competition and  
756 predation (including marine mammals) on Pacific Herring stocks.

757

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768

## 769 **FIGURE AND TABLE CAPTIONS**

770 **Table 1** List of physical and biological descriptors used in the single-species Poisson-link *VAST*  
771 delta-model fitted to Pacific Herring data.

772 **Table 2** Parameters for single-species and multi-species *VAST* models.

773 **Figure 1** Spatio-temporal dynamics of Pacific Herring (*Clupea pallasii*) biomass estimated from the  
774 summer pelagic survey off the West Coast of Vancouver Island (WCVI), 2006-2014. These  
775 dynamics were inferred by fitting a single-species spatio-temporal Poisson-link delta model to  
776 this fisheries-independent survey data. Estimated Pacific Herring densities for every knot/year  
777 combination are mapped (A) and estimated relative abundance index values are plotted by year  
778 (B). To obtain a relative index without units, the *VAST*-derived abundance indices (and standard  
779 errors) were divided by the mean of all abundance indexes. In (C), there is a map of WCVI area.

780 **Figure 2** Predicted effects of May sea surface temperature (May SST) on log-transformed Pacific  
781 Herring biomass derived from a single-species Poisson-link *VAST* delta-model fitted to Pacific

782 Herring data. Plots were drawn from the most parsimonious model according to a stepwise  
783 procedure investigating covariate effect on two components of the delta-model.

784 **Figure 3** Representation of the first two factors for spatial variation in the 1<sup>st</sup> linear predictor of  
785 a Poisson-link *VAST* delta model for Pacific Herring and seven groundfish species off the West  
786 Coast of Vancouver Island, 2006-2014. Maps are represented in (A) while species' loadings are  
787 represented in (B).

788 **Figure 4** Analytic estimates of correlation among Pacific Herring and seven groundfish species off  
789 the West Coast of Vancouver Island over the period 2006-2014 for spatial and spatio-temporal  
790 variation in the 1<sup>st</sup> linear predictor of a Poisson-link *VAST* delta model. All correlations are  
791 significant according to a Wald test (significance level: 0.05).

792 **Figure 5** Representation of the two first factors for spatio-temporal variation in the 1<sup>st</sup> linear  
793 predictor of a Poisson-link *VAST* delta model for Pacific Herring and seven groundfish species off  
794 the West Coast of Vancouver Island for the years 2006, 2008, 2010, 2012 and 2014. Maps are  
795 represented in (A) while species' loadings are represented in (B).

796 **Figure 6** Representation of the first two factors for spatial variation in both linear predictors of a  
797 Poisson-link *VAST* delta model for Pacific Herring and six pelagic, competitor fish species off the  
798 West Coast of Vancouver Island, 2006-2014. Maps are represented in (A) while species' loadings  
799 are represented in (B).

800 **Figure 7** Analytic estimates of correlation among Pacific Herring and six pelagic, competitor fish  
801 species off the West Coast of Vancouver Island over the period 2006-2014 for spatial and spatio-  
802 temporal variation in both linear predictors of a Poisson-link *VAST* delta model. All correlations  
803 are significant according to a Wald test (significance level: 0.05).

804 **Figure 8** Representation of the first two factors for spatio-temporal variation in both linear  
805 predictors of a Poisson-link *VAST* delta model for Pacific Herring and six pelagic, competitor fish  
806 species off the West Coast of Vancouver Island for the years 2006, 2008, 2010, 2012 and 2014.  
807 Maps are represented in (A) while species' loadings are represented in (B).

808 **Figure 9** (A) Representation of the first factor for spatial variation in the 1<sup>st</sup> linear predictor of a  
809 Poisson-link VAST delta model for Pacific Herring, Pacific Hake, Euphausiids and preferred  
810 zooplankton prey of Herring off the West Coast of Vancouver Island for the years 2009, 2011,  
811 2012, 2013. Species' loadings are represented in (B). Analytic estimates of correlation for spatial  
812 variation and spatio-temporal variation among those species are represented in (C) and (D);  
813 Statistically insignificant correlation and covariance estimates based on a significance Wald test  
814 are symbolized by white cross.

815

## 816 **SUPPLEMENTARY INFORMATION**

817 **Appendix S1A** Sampling stations for the pelagic survey for years 2006, 2008-2014 off the West  
818 Coast of Vancouver Island.

819 **Appendix S1B** Sampling stations for the groundfish survey for years 2006, 2008, 2010, 2012 and  
820 2014 off the West Coast of Vancouver Island.

821 **Appendix S1C** Sampling stations for the acoustics-based Pacific Hake survey for years 2009, 2011,  
822 2012 and 2014 off the West Coast of Vancouver Island. These surveys were conducted in August  
823 and September, and involved collecting acoustic data along parallel transects spaced 10 or 20  
824 nautical miles apart off WCVI.

825 **Appendix S2** List of 40 zooplankton species known to be prey of herring off the West Coast of  
826 Vancouver Island.

827 **Appendix S3** MODIS-derived shelf-wide indexes of SST for years 2003-2015 off the West Coast of  
828 Vancouver Island.

829 **Appendix S4** Single-species VAST-derived predicted relative abundance index for Pacific Hake for  
830 years 2009-2013.

831 **Appendix S5** VAST-derived estimated relative abundance index for Pacific Herring prey  
832 (zooplankton) for years 2009-2014.

833

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